

Prey, Predatory Behavior, and the Daily Cycle of *Holopogon wilcoxi* Martin

(Diptera: Asilidae)

Henry A. Hespenheide and Mark A. Rubke

Department of Biology
University of California Los Angeles, 90024

The literature on the Asilidae has taken several points of view on robberflies as predators: The ethology of the act of predation (Lavigne and Holland 1969, Dennis *et al.* 1975), diurnal activity pattern (Dennis and Lavigne 1975) seasonal and microhabitat selection (Scarborough 1974), selection of prey by type (Linsley 1960, Powell and Stage 1962), and by size (Lavigne and Holland 1969, Dennis and Lavigne 1975, Hespenheide 1975:82). Studies of other organisms which prey on flying insects and the prey available to them have revealed that there is a strong diurnal periodicity in prey availability (Hespenheide 1975; Lewis and Taylor 1964). Because of the ease of observing predatory behavior in robberflies and the location of a locally large population of *Holopogon wilcoxi*, the present study was undertaken to determine the diurnal pattern of foraging in this species. Other aspects of the behavior of this species were also noted, and an analysis was made of the prey taken. *Holopogon wilcoxi* perches on the tips of branches and sallies out after small insects which fly nearby. The overall behavior of *Holopogon wilcoxi* is similar to that recorded for species of *Heteropogon* (Lavigne 1970:270, Lavigne and Holland 1969) and *Holopogon albipilosus* (Dennis and Lavigne 1975).

Methods

Holopogon wilcoxi was censused hourly along a standard path in an area of approximately 20 by 35 meters (see description of study area, below). The day was divided into nine one-hour periods between 8 and 17 hrs, and each period was censused on three separate days during the period 25 to 30 May 1975. The total number of *Holopogon* seen was recorded as well as the number with prey. Those with prey were caught, when possible, in a small plastic vial, and then released after the prey was dropped, usually immediately. The prey item was then transferred to alcohol in the field. Because of the relatively small sample sizes, the prey specimens in alcohol were accumulated by two-hour time periods, and no distinction was made among the days of collection. Prey items were subsequently sorted to species and

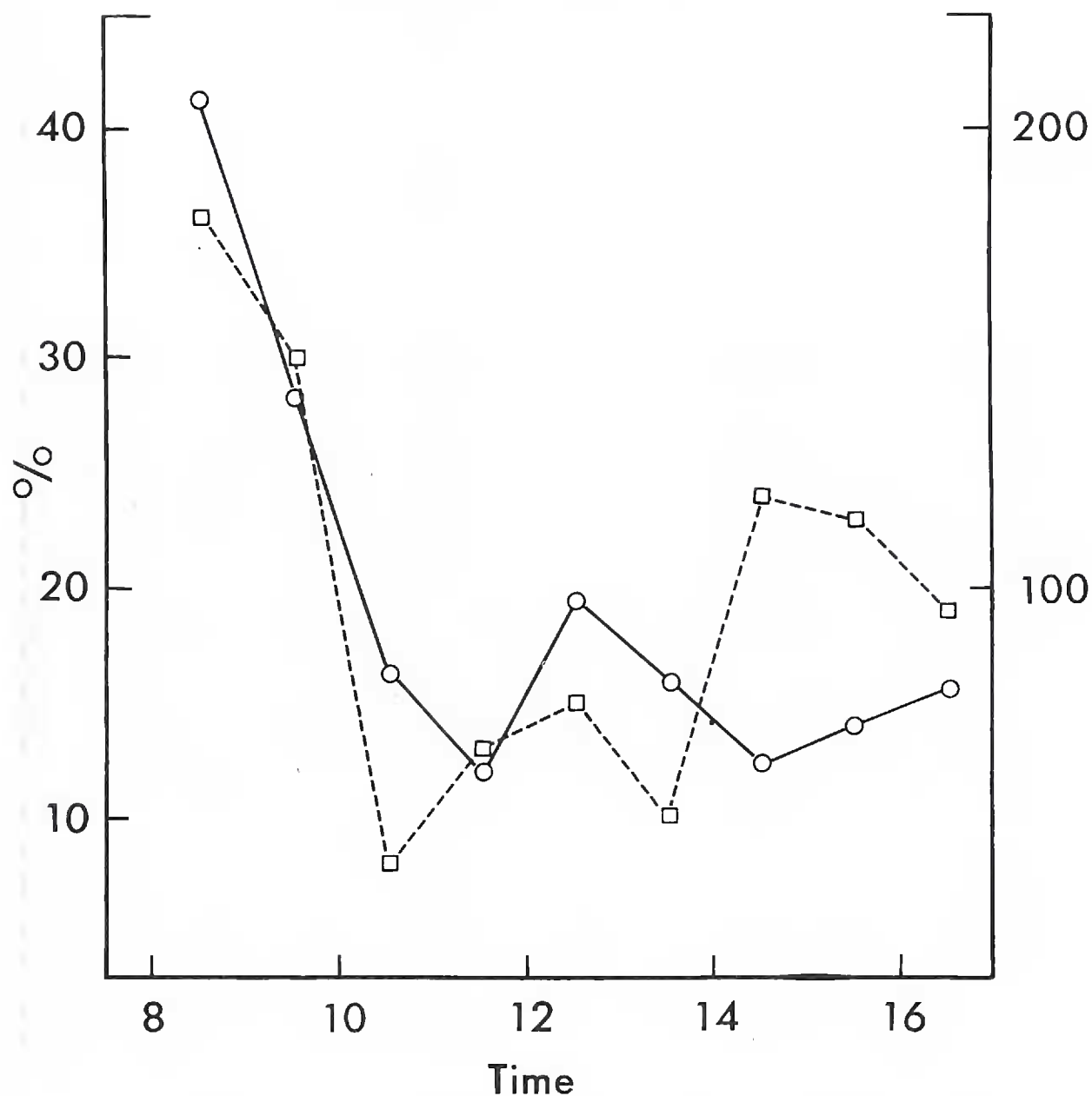


Fig. 1. Diurnal changes in numbers of *Holopogon wilcoxi* and proportion of individuals with prey. Right ordinate and solid line show changes in number of flies, expressed as the sum of three censuses; left ordinate and dotted line, per cent of flies observed with prey; abscissa in hrs.

measured for body length (excluding wings) in the laboratory. Prey length was used as an index of prey size, and size data were analyzed statistically.

An attempt to measure flying insect density and diversity — i.e., insects available as prey to *Holopogon* — by means of sweep samples proved unsuccessful, as all samples were very small. Many general observations on behavior were also made in the field.

Study Site

The study was conducted along the north and west side of the road through the lower part of Cave Creek Canyon in the Coronado

National Forest, Cochise County, Arizona, about 2 mi sw of Portal at about 5000 feet elevation. The site was located at the base of the steep southeast-facing wall of the canyon about 40 m from Cave Creek. The study area was relatively open, with *Mimosa biuncifera* Benth. as the dominant shrubby vegetation, 0.5 to 3 m tall, and with several species of oaks (*Quercus* spp.) roughly bounding the area. *Mimosa* was largely leafless because it is seasonally deciduous and was, as a result, the most common plant used for perches, although exposed oak twigs and those of the few sumacs (*Rhus* sp.) present were also used.

Results and Discussion

Diurnal Feeding Periodicity: Mid-morning (8 to 10 hours) proved to be the preferred time of day for feeding activity, measured by the number of flies with prey (Figure 1). This was also the time of day when the greatest number of asilids were present in the study area, in turn probably a response to the greatest prey availability. The number of flies feeding is significantly correlated with the number present — the correlation coefficient $r = 0.733$, with a probability between .05 and .02 that the correlation is due to chance. Other studies (Lavigne and Holland 1969) have pointed out that the density of available prey was reduced when the air temperature was either very cool (early morning) or very hot (midday). Published data for flight periods of a variety of insects (Hespenheide 1975:82 Lewis and Taylor 1964) show insects are more often active during early to mid-morning. The importance of temperature is suggested by the observation that during one particularly cool mid-morning period (not censused) following a late-afternoon rain the preceding day, very few asilids were present in the area, and none of those had captured prey, this in strong contrast with a typical mid-morning period. (Fig. 1).

The diurnal cycle of feeding by *Holopogon wilcoxi* differs somewhat from that typical of mid-summer species studied by Lavigne and Holland (1969). There is a similar morning peak, but then a mid- instead of late-afternoon rise (Fig. 1). The reason for a mid-afternoon rise is unclear. It was still quite warm at 14 hrs and nearly as warm at 15 hrs; few asilids were in the area, but nearly 25% had prey. The low density of *Holopogon* might indicate prey density was still low because of the warm temperatures, but for some reason the asilids were more efficient in foraging during this period, perhaps because of light conditions and the flies' use of backlighting to detect prey (Lavigne, personal communication, and below).

One might expect a rise in late-afternoon foraging activity when the temperature cools to that at which prey activity is once again high. That this was not observed was likely due to winds which developed each afternoon. The winds impaired prey flight activity as well as



Fig. 2. *Holopogon wilcoxi* in "sleeping" position, about 7:30 hrs.

efficiency of foraging by *Holopogon*, and few asilids were seen flying in the late afternoon hours. This has been found to be true of other species of asilids as well (Lavigne and Holland 1969). Prey become relatively scarce during windy weather, for only the stronger fliers are able to cope with it (Johnson 1950).

The phenomenon of moving into an area during the day and out again at dusk or earlier, as in the case of *Holopogon*, has been observed for other asilid species, even when present in dense populations (Lavigne and Holland 1969). In the present study it was not determined where the majority of the asilids passed the night, and the reason for moving out of the area daily therefore remains unclear. Perhaps they move to an area where the sunlight will hit them earliest in the morning and then fly to areas better suited for foraging.

Holopogon wilcoxi always perches in the sun when active. If the sun is blocked by a hand that is even relatively far away, the fly will immediately move to another perch. This, too, has been shown for *Heteropogon maculinervis* and *Backomyia* (Lavigne 1970:270, 1971). This observation and the pattern of foraging behavior suggest the great importance of temperature on the diurnal cycle of *Holopogon*. Ambient temperature, combined with heat derived from direct insolation, appears to be the most important physical factor of the environment to which the flies react.

Lavigne (1970:270) reports *Heteropogon maculinervis* pressing their bodies against the longitudinal axis of a branch during cooler, cloudy weather. Similar behavior was observed for *Holopogon wilcoxi*. Both in the evening and in the early morning the flies could be seen



Fig. 3. *Holopogon wilcoxi* in typical foraging position, feeding on prey, probably a psyllid.

assuming various positions in which the head of the fly is pressed down close to the twig. These are believed to be "sleeping" positions of the flies and to be elicited by cool temperatures. The position has the effect of making the fly cryptic, in that the fly appears to be a thorn or an extension of the perch twig with the black abdomen characteristically protruding away from the twig. The crypticity could be beneficial, in that once a fly becomes cool it is essentially immobile and is vulnerable to predation. However, no predators of *Holopogon* were observed.

Prey Selection

Like most other asilid species, *Holopogon wilcoxi* captures prey on the wing by sallying out from a perch and then returning with the prey to a perch. (Fig. 3). Foraging flights were observed to be between 7-8 cm and a meter in length. The flies would often not capture an intended prey individual, but would almost always return to the same perch. The perches were from about .3 to 3 m above the ground, with most between 1 and 1.5 m. When another insect flies by, even a very large one or a conspecific, the flies turn their entire body to view it, similar to behavior exhibited by *Holopogon albipilosus* (Dennis and Lavigne 1975). Occasionally a fly was observed to move to another perch or to fly out of the immediate area altogether after a long period of inactivity on its original perch. This suggests that flies will move to

a different perch or area if prey activity is insufficient in the immediate vicinity, an observation also made by Lavigne and Holland (1969).

The types, numbers, and sizes of prey taken are given in Table 1. Because sampling of insects available to *Holopogon* as prey proved unfeasible, it is impossible to discuss prey selection directly. The predominant insect prey taken were Homoptera of the families Cicadellidae, Psyllidae and Aphididae. Diptera and Hemiptera each also accounted for more than 10% of the total prey items; Hymenoptera, Coleoptera, Thysanoptera and Lepidoptera accounted for less than 5% each. Among published records of prey taken by other North American Asilidae, only species of *Backomyia* (50 and 58%, Lavigne 1971) and *Asilus mesae* (57%, Dennis and Lavigne 1975) show comparable proportions of Homoptera taken as prey. Homoptera, especially aphids, have been shown by some studies to predominate among samples of flying insects, although most studies show Diptera to be the most common order (review in Hespeneide 1975:82). Small Diptera were the second most frequent prey item, both in numbers of individuals and species. Hemiptera were next most common as individuals, but no more common in number of species than Hymenoptera or Coleoptera, which suggests that *Holopogon* preyed on locally abundant populations. Of the four orders taken only occasionally, thrips seem not to be recorded as prey items of asilids previous to this study.

That different taxa of insects have different preferred activity periods (Hespeneide 1975:82 and included references) is borne out by a comparison of prey taken by *Holopogon* at different time of the day. The ordinal composition of 76 prey items taken between 8 and 10 hrs is different from the composition of 45 prey items taken by the flies during the rest of the day (10 to 17 hrs; although not significantly so [$\chi^2 = 5.85$, $0.5 > \text{probability of } \chi^2 > 0.1$]). This demonstration of hour-to-hour differences in diet of a hunting predator suggests the importance of taking time of day into account in quantitative studies of prey selection (discussed in Hespeneide 1975:82).

Although size has regularly been shown to be an important characteristic of prey to predators (review in Hespeneide 1973), comparison of mean sizes among the orders of prey reveals that *Holopogon* prefers significantly different sizes of prey from one order compared to those from another, an observation that has been made of other species of asilids, as well as birds (Hespeneide 1975:158). Prey size is almost certainly important, but not in a simple way. Minimum observed prey size was about 0.4 mm for an aphid, and many prey were less than 1 mm long. It is of particular interest to note that maximum prey size in *Holopogon wilcoxi* seems to be limited to that which still allows the fly to alight on its perch. A number of times

Table 1. Prey of *Holopogon wilcoxi*

Taxon	Number total (%)	measured	species	Size — untransformed			— transformed ¹			Significance of difference in means ³								
				$\bar{x} \pm se$	g_1^2	g_2	$\bar{x} \pm se$	g_1	g_2	Ho-C	-P	-A	D	He	Hy	C	T	
Homoptera	72 (59.5)	65	18	1.16 ± .06	+	+	1.02 ± .02	0	0									
Cicadellidae	24	23	6	1.09 ± .15	+	0	0.96 ± .03	+	0	-	+	-	+	++	++	-	-	
Psyllidae	16	16	7	1.32 ± .08	0	0	1.10 ± .03	+	0	-	-	-	++	-	++	-	-	
Aphididae	32	26	5	1.11 ± .06	0	0	1.03 ± .03	+	+	-	+	-	++	+	++	-	-	
Diptera	18 (14.8)	17	11	1.45 ± .15	0	0	1.12 ± .04	0	0	-	-	+	-	++	-	+	-	
Hemiptera	17 (14.0)	17	5	2.33 ± .15	0	0	1.35 ± .03	0	0	++	++	++	++	-	+	-	++	
Hymenoptera	5 (4.1)	5	4	1.58 ± .26	+	+	1.18 ± .06	+	0	-	-	-	-	+	-	-	-	
Coleoptera	4 (3.3)	4	4	1.92 ± .23	0	0	1.28 ± .05	0	0	++	+	++	-	-	-	-	+	
Thysanoptera	4 (3.3)	4	3	1.10 ± .17	0	0	1.03 ± .06	0	0	-	-	-	-	++	-	+	-	
Lepidoptera	1 (0.9)	1	1	2.2			1.34											
Total	121	113	44	1.43 ± .06	+	0	1.11 ± .02	0	0									

¹ \log_{10} (size x 10)² g_1 and g_2 are statistics testing significance (+) of skewness and kurtosis, respectively.³ + = significant at .05 level; ++ = significant at .01 level; above the diagonal are comparisons of transformed means, below are comparisons of untransformed means.

an asilid was observed to capture a prey item two or three times its size, only to drop it finally because it could not land with it. The overall range of prey sizes is between 1/10 and 1/2 the length of the fly, similar to that of other species (Lavigne and Holland 1969).

For aerially-foraging birds it has been proposed that choice of prey is based partly on overall ease or difficulty of capture and partly on local prey density (Hespenheide 1975:82), and the same combination has been proposed to explain prey preference in the asilid *Stenopogon engelhardti* by Powell and Stage (1962). For most organisms, flight speed and agility is an increasing function of body size, so that a predator will almost always have an advantage over a relatively smaller prey. The smaller Homoptera, particularly the aphids, and the Diptera are especially weak fliers and therefore more vulnerable as prey. The high frequency of certain species as prey of *Holopogon* suggests that differences in availability, expressed as local concentrations of individuals of these species, were important, although these could not be measured effectively for this study. Toughness of the prey integument may be an additional factor. Of the prey items most often caught, the Homopterans and Diptera are both characteristically soft-bodied.

Acknowledgments

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SCIENTIFIC NOTE

Collection of a Larva of the Incense Cedar Woodwasp, *Syntexis libocedrii* (Rohwer, 1915) from Pioneer, Amador County, California. (Hymenoptera: Syntexidae) — *Syntexis libocedrii*, the monotype of the Family Syntexidae, heretofore has been reported from northern California in the Sierra, Siskiyou and Cascade ranges to southern Oregon (R.B. Benson, 1935; Ann. Mag. Nat. Hist.; 16:535-553; W. W. Middlekauff, 1974; Pan-Pacific Entomol. 50(3):288-290; B. E. Wickman, 1967; Ann. Entomol. Soc. Amer. 60(6):1291-1295; R. L. Wescott, 1971; Pan-Pacific Entomol. 47:310).

On 26 July 1977 a dessicated larva of *S. libocedrii* was recovered from approximately 2 cm into the sapwood of an 83 to 90 cm diameter Incense Cedar log (*Libocedrus decurrens* Torr.). The log was topmost in a deck of cedar logged from the Stanislaus National Forest in early 1977 and stored at the sawmill of California Mills, Inc. at Pioneer, California. Our tentative identification of the badly dessicated larva was confirmed by Dr. W.W. Middlekauff of the Dept. of Entomology at the University of California, Berkeley, who originally described the larvae of *S. libocedrii* (Middlekauff, 1974; Pan-Pacific Entomol. 50(3):288-290.)

Collection of this larva represents the first recorded occurrence of *S. libocedrii* this far south in California, although Wickman (1967; Ann. Entomol. Soc. Amer. 60(6):1291-1295) conceded that *S. libocedrii* probably occurs throughout the range of *L. decurrens* (southern Oregon to northern Lower California and east into western Nevada) (P.A. Munz, 1959; *A California Flora with Supplement*; U. Cal. Press; Berkeley, California, pp. 59). — L.W. TURLINGTON, S.F. COOK, Dept. of Biological Sciences, University of the Pacific, Stockton, California 95211.